Vision Research 63 (2012) 9–19

Contents lists available at SciVerse ScienceDirect

Vision Research

journal homepage: www.elsevier.com/locate/visres

The frequency of horizontal saccades in near and far symmetrical disparity vergence

Eun H. Kim, Tara L. Alvarez *

Department of Biomedical Engineering, New Jersey Institute of Technology, Newark, NJ 07102, USA

ARTICLE INFO

Article history:
Received 29 November 2011
Received in revised form 27 March 2012
Available online 7 May 2012

Keywords:
Binocular vision
Version
Oculomotor
Vergence
Conjugate
Saccade

ABSTRACT

In a natural environment, saccade and vergence eye movements shift gaze in different directions and distances. In a laboratory setting, targets can be positioned precisely to elicit symmetrical vergence movements; however, saccades occur during the vergence movement even though the stimulus should not stimulate a saccadic response. These saccades may facilitate the response when the kinematics of the vergence component are modest as indicated by reduced velocities. Hence, the purpose of this study is to assess whether the frequency of saccades within vergence responses are correlated with vergence peak velocity. Ten subjects with normal binocular vision participated in this study. Eye movements were quantified using a limbus tracking system. Stimuli included 4° symmetrical convergence and divergence steps with an initial vergence angle at far (2° and 6°, respectively) and near (12° and 16°, respectively) which are known to evoke different vergence peak velocities. A saccade detecting algorithm was utilized to compute the percentage of saccades present within all vergence responses. A repeated measures ANOVA confirmed with a post hoc Bonferroni test demonstrated that convergence steps at near were slower than convergence steps at far, whereas divergence steps at far were slower than divergence steps at near in all subjects ($p < 0.02$). When the vergence peak velocity was slow, a greater number of saccades was observed. The average vergence peak velocities were inversely correlated to the number of saccades observed within the transient portion defined as after the latency to 400 ms of the movement ($r = -0.41$; $p = 0.008$), between 400 ms and 1 s of the response ($r = -0.35$; $p = 0.03$) and within the steady-state period occurring between 1 s and 3 s of the response ($r = -0.44$; $p = 0.005$). Peak velocity of vergence is dependent on the stimulus initial vergence angle. An increased prevalence of saccades was observed in vergence responses with reduced peak velocity, compared to responses with greater peak velocity. Prior research supports that saccades increase the peak velocity of vergence during combined vergence and saccadic tasks. This may in part explain the increased presence of saccades within vergence responses with reduced peak velocities. The recruitment of saccades may be utilized because of the longer period of diplopia resulting from slower vergence movements.

1. Introduction

A horizontal saccadic response is a type of version or conjugate movement that rapidly shifts the eyes in tandem. Convergence and divergence (disjunctive or vergence movements) are the inward and outward rotation of the eyes respectively, responsible for the perception of spatial depth. Under natural conditions, the visual system uses a combination of version and vergence eye movements (Busettini & Mays, 2005a, 2005b; Kumar et al., 2005; Malinov et al., 2000; Qing & Kapoula, 2004; van Leeuwen, Collewijn, & Erkelens, 1998; Zee, Fitzgibbon, & Optican, 1992). Both version and vergence movements are critical, especially when a person is engaged in tasks that utilize sustained near work such as reading or computer use. With the increased prevalence within our society of small interface devices, such as smart phones and tablets, the demand for both saccade and vergence eye movements are increasing within our daily activities. Furthermore, clinicians are reporting an increase in visual symptoms associated with sustained near work (Bababekova et al., 2011; Hoffman et al., 2008; Howarth, 2011); yet, only a few studies have investigated the etiology of these symptoms (Collier & Rosenfield, 2011; Ishikawa, 1990; Rosenfield, 2011). This study quantifies the frequency of horizontal saccades in symmetrical vergence eye movements that are prevalent in both near and far visual tasks.

Convergence typically occurs with other eye movements. However, it is possible to elicit a pure disparity vergence stimulus by precisely positioning visual targets along the subject's midline. Our laboratory and other investigators have published that even when symmetrical vergence stimuli are presented to a subject, many of the responses contain horizontal saccades (Coubard & Kapoula, 2008; Semmlow et al., 2008, 2009). Coubard and Kapoula (2008) characterized saccades during symmetrical 8.2° convergence steps and 6.2° divergence steps with an initial vergence

* Corresponding author. Fax: +1 973 596 5222.
E-mail address: tara.l.alvarez@njit.edu (T.L. Alvarez).

0042-6989/$ - see front matter © 2012 Elsevier Ltd. All rights reserved.
http://dx.doi.org/10.1016/j.visres.2012.04.013

angle of 8.5°. They reported that saccades were found in up to 84% of the vergence responses and identified six morphologies of the saccadic components. Ying and Zee (2006) reported differences in the timing and amplitude of the saccades within divergence movements after short and long periods of sustained symmetrical convergence (Ying & Zee, 2006). Semmlow and colleagues et al. (2008) demonstrated that the initial saccades occurred in a preferred direction (leftward or rightward) during 4° symmetrical vergence responses (Semmlow et al., 2008). These investigators concluded that horizontal saccades in symmetrical vergence tend to quickly bring one eye closer to the target since saccadic peak velocities are typically an order of magnitude faster than vergence peak velocities (Coubard & Kapoula, 2008; Semmlow et al., 2008, 2009; Ying & Zee, 2006). Furthermore, as the aforementioned studies report, saccades are commonly observed in symmetrical vergence when the visual input does not directly stimulate a conjugate response.

The speed of vergence has an impact on a person's activities of daily living. For example, one study on repetitive vergence movements, analogous to performing visual tasks for a prolonged period of time, reports an average reduction of 20% in vergence peak velocity (comparing the responses from the beginning to those recorded at the end of the session) (Yuan & Semmlow, 2000). In addition, quantitative studies have reported that convergence peak velocity is significantly reduced compared to age matched controls when a person has a vergence dysfunction known as convergence insufficiency (Alvarez et al., 2010; Thiagarajan, Ciuffreda, & Ludlam, 2011). None of these studies conducted a systematic investigation of the relationship between the vergence peak velocity and the prevalence of saccades commonly observed within symmetrical vergence responses. We propose that conducting this analysis will yield insight into how the vergence system may compensate for slow velocity movements. This is relevant because the vergence peak velocity can be significantly reduced as a result of fatigue and/or vergence dysfunction (Alvarez et al., 2010; Yuan & Semmlow, 2000).

Studies have not yet investigated the prevalence of saccades within responses to symmetrical vergence stimuli located at different initial vergence angles (near versus far) to analyze whether a correlation exists between the speed of the vergence movement and the number of saccades generated within the response. Thus, the purpose of the current study is to investigate whether the frequency of saccades during symmetrical vergence movements is dependent on vergence peak velocities. A within-subject design can be engineered to elicit vergence responses with different peak velocities. Both models and empirical data support that divergence responses at far will be slower than divergence responses at near, and convergence responses at near will be slower than those at far (Kim et al., 2010, 2011; Lee et al., 2009; Patel, Jiang, & Ogmen, 2001; Patel et al., 1997). By employing a within-subject experimental design using the four vergence step stimuli (convergence and divergence steps at near and far initial vergence angles), we will test our hypothesis that responses with slower vergence peak velocities will contain a greater number of saccades compared to those that have faster kinematics.

2. Methods

2.1. Subjects

Ten subjects (5 males, 5 females) without a history of brain dysfunction or injury participated in this study. Subjects were between 20 and 31 years of age with a mean and standard deviation of 22.9 ± 3.1 years. All subjects had an NPC less than 6 cm and normal binocular vision defined as better than 50 s of arc assessed by the Randot Stereopsis Test (Bernell Corp., South Bend, IN, USA) using methods described in detail in our previous research (Alvarez et al., 2010). All subjects were emmetropes except for subjects S1 and S9 who were myopes (1.75 ± 0.71 D) and were corrected for refractive error during the experiment. This study was approved by the New Jersey Institute of Technology Institute Review Board in accordance with the Declaration of Helsinki prior to the experiment. All subjects gave informed written consent.

2.2. Measurement of eye movements and visual stimuli

Eye movements were recorded using an infrared (λ = 950 nm) system manufactured by Skalar Iris (Model 6500, Netherlands). The eye movement responses were within the linear range of the system (±25°). Visual stimuli were displayed using a haploscope where two computer screens were used to generate a symmetrical (identical in shape, light intensity and color) disparity vergence stimulus along the subject's midline. The stimulus, a green vertical line 2 cm in height and 2 mm in width, was presented on a black background. Two partially reflecting mirrors projected the two vertical lines from the computer screens into the subject's line of sight. The stimuli from the computer screens were adjusted with the mirrors to calibrate the visual stimulus with real targets located at measured distances from the subject's midline prior to data collection. An inter-pupillary distance of 6 cm was assumed. The stimuli monitors were placed 40 cm away from the subject, hence the accommodative stimulus was held constant. During the experiment, only the visual stimulus displayed on the computer screen was seen by the subject. The subject's head was restrained using a custom chin rest to eliminate head movement and avoid any vestibular influences during the experiment.

The left-eye and right-eye responses were recorded, calibrated, and saved separately for offline data analysis. Digitization of eye movement data were performed using a 12-bit digital acquisition (DAQ) hardware card with a range of ±5 V (National Instruments 6024 E series, Austin, TX, USA). The entire system was controlled by a custom LabVIEW™ 8.0 program (National Instrument, Austin, TX, USA) which generated the visual stimuli and digitized the eye movement data sampling at a rate of 200 Hz (Guo, Kim, & Alvarez, 2011).

2.3. Experimental protocol

The vergence step stimuli were near convergence steps (12° initial vergence angle), far convergence steps (2° initial vergence angle), near divergence steps (16° initial vergence angle) and far divergence steps (6° initial vergence angle). The vergence step stimuli were randomly intermixed and presented after a random delay between 0.5 and 2.0 s to avoid prediction which is known to enhance vergence peak velocities (Alvarez et al., 2005, 2002). Due to the randomization algorithm, approximately 25–30 responses of each stimulus were collected for data analysis. At a minimum, 25 responses were collected of each stimulus type.

2.4. Data analysis

Vergence data were calibrated using two-points, the initial and final vergence position demand of the vergence step stimuli similar to our past study (Kim et al., 2010). Our system has a high degree of linearity, within 3% between ±25° horizontally (Horng et al., 1998). Vergence was calculated by subtracting the right-eye response from the left-eye response to yield a net vergence response. Conjugate or version was calculated by averaging the right-eye response and the left-eye response. Vergence and conjugate velocity traces were computed using a two-point central difference algorithm (Bahill, Kallman, & Lieberman, 1982). Convergence responses were plotted as positive while divergence responses were plotted as negative.

Responses with blinks at any point during the vergence movement were omitted from the analysis. A phase plot (vergence velocity as a function of vergence amplitude) was used to determine whether the saccades obscured the peak velocity of the vergence response to a symmetrical stimulus. When saccades obstructed the vergence peak velocity then the response was omitted from the vergence peak velocity analysis. Examples of vergence responses with and without saccades and the corresponding phase plots that were accepted for vergence peak velocity analyses are shown in Fig. 1.

Saccades within the symmetrical vergence responses were detected by using a semi-automated custom software program written in MATLAB (Semmlow et al., 2008, 2009). Using the conjugate position trace, any saccades that were greater than 0.15° in magnitude were identified by the software. The responses were also manually inspected by the operator. The conjugate magnitude and direction were quantified and used to categorize whether the saccade induced or reduced the error between the current position of the eyes and the stimulus target. Semmlow and colleagues et al. (2009) have shown that the initial saccade induces an asymmetric error where one eye is within the line of fixation (along midline) while the other eye is not. This type of saccade is called an error-inducing saccade. Then, typically a secondary saccade is subsequently initiated and reduces the error by attempting to bring both eyes into the line of fixation. This type of saccade is called an error-reducing saccade (Semmlow et al., 2008). We quantified the number of error-reducing saccades compensating for the error induced by the initial saccade. In addition, the onset time (s) of the initial saccades relative to the vergence response were measured. Examples of two responses showing the right eye, left eye, vergence and conjugate position traces, as well as the vergence and conjugate velocity traces from two different subjects, are shown in Fig. 2 plots A and B.

2.5. Statistical analysis

Statistical comparisons were performed using a paired *t*-test. A repeated measures ANOVA was also used to determine whether

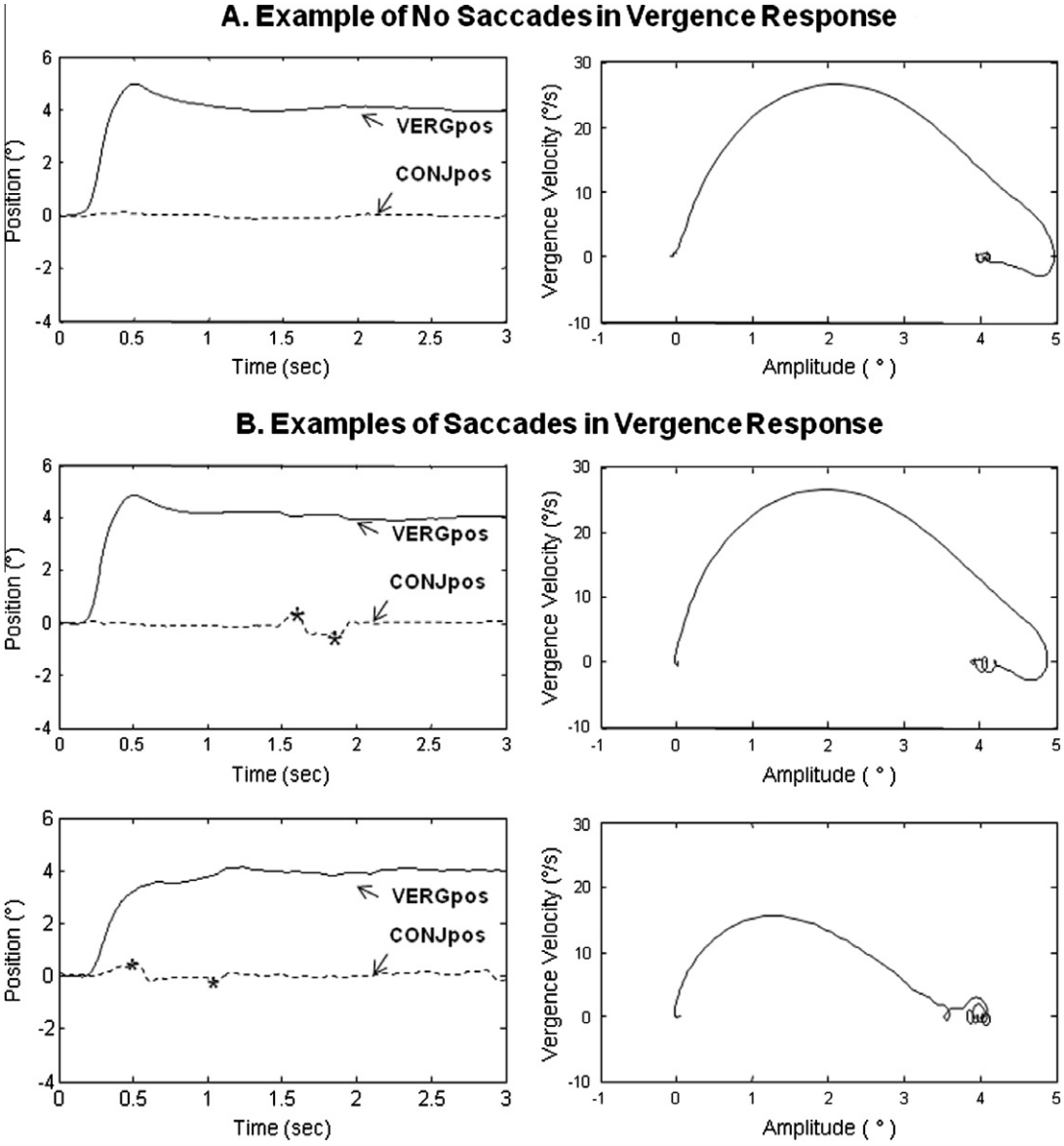

Fig. 1. Vergence peak velocities were analyzed using the phase plot (right column). The first row, left plot is an example of vergence (VERGpos) and version (CONJpos) position traces without the presence of saccades. The corresponding phase plot is shown in the first row, right plot. The second and third rows, left plots are examples of vergence responses with saccades. The saccades are indicated by the symbol '*'. However, the phase plot demonstrates that the saccades that are present within these vergence responses do not obscure the vergence peak velocity observed within the phase plot.

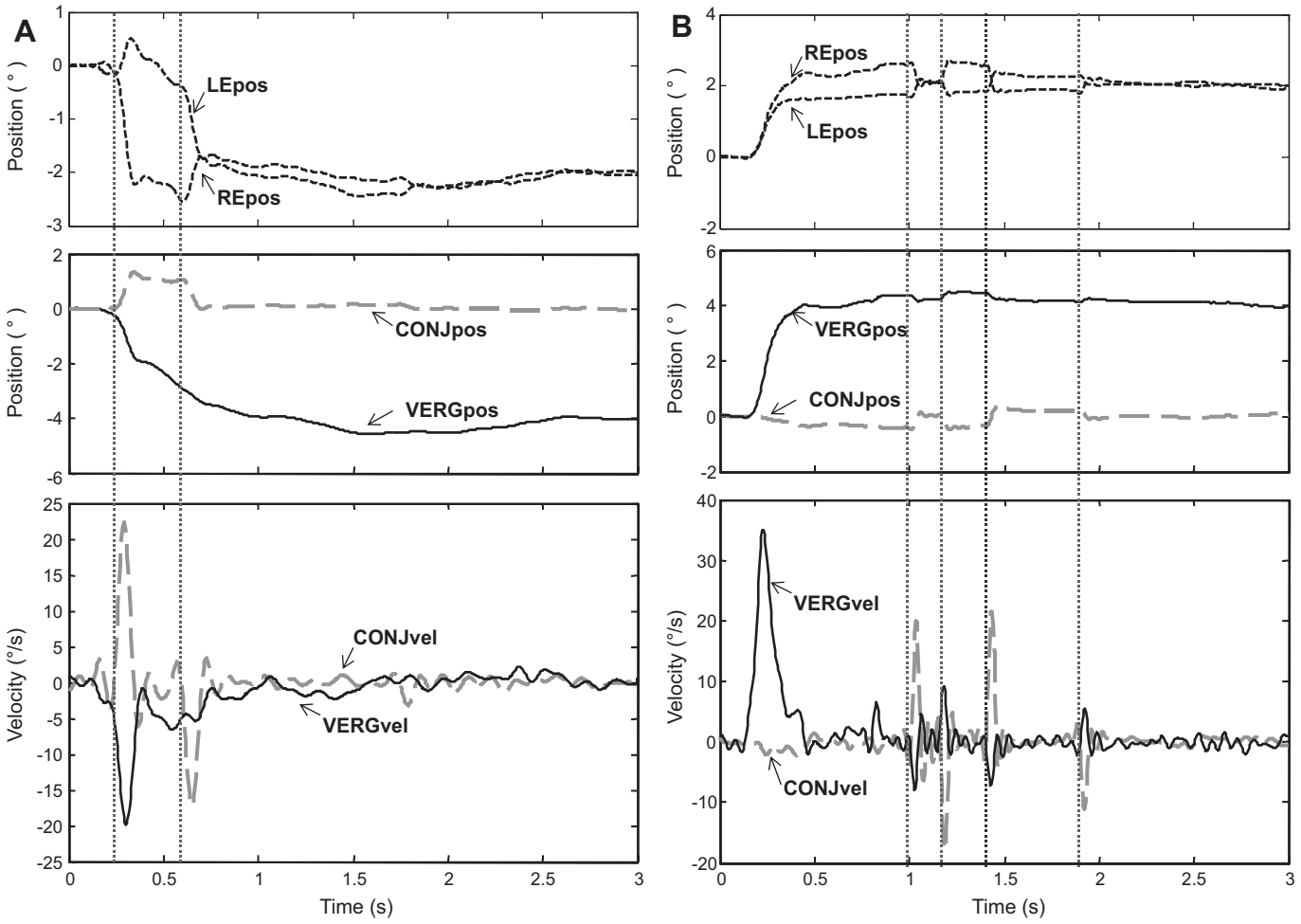

Fig. 2. Individual example of a single divergence response from subject S2 (plot A) and convergence response from S10 (plot B). The conjugate response (CONJ gray dashed lines) and vergence response (VERG black solid lines) are represented as the average of the two eyes (left eye LE and right eye RE) and the difference of the left and right eye respectively. The onset of a saccade is aligned with a thin dotted line identified using the conjugate velocity trace (CONJvel). Saccades may be present in the early transient portion of the vergence response shown in plot A or saccades may be present in the latter portion of the vergence response shown in plot B. Position traces (CONJpos, conjugate or version; VERGpos, vergence; REpos, right eye position; LEpos, left eye position), and velocity traces (VERGvel, vergence velocity; CONJvel, conjugate velocity) are also shown. There are two saccades present in divergence in subject S2 while four saccades are present in convergence in subject S10.

the peak velocity of vergence and the onset time of the initial saccades were significantly dependent upon (1) the initial vergence angle (near versus far) and/or (2) the direction of the vergence responses (convergence versus divergence). In addition, a repeated measures ANOVA was used to determine whether the latency of vergence responses were dependent on the initial vergence angle. NSC2004 (Kaysville, UT, USA) software was used for statistical calculations.

A linear regression analysis calculated with MATLAB™ software (Waltham, MA, USA) was used to assess the correlation between the average vergence peak velocities and the percent of saccades in all vergence responses during (1) the transient portion (saccades occurring after the vergence latency, assessed as the time when movement begins up to 400 ms of the vergence responses), (2) from 400 ms to 1 s of the movement and (3) between 1 s and 3 s. We selected these three time durations because a previous study demonstrates that an initial saccade (the error-inducing saccade) typically occurs during the transient portion of the vergence response (less than 400 ms). An error-reducing saccade will subsequently follow the initial saccade after the transient portion of the response and typically an error-reducing saccade will occur within 1 s of the ongoing vergence response (Semmlow et al., 2008). The last analysis (between 1 and 3 s) quantifies saccades occurring within the steady state portion of the response. The percentage of saccade was used because subjects did not have the same number of convergence and divergence at near and far responses due to the randomization algorithm of our data acquisition software. For example, when 100% saccades were observed, it means that on average one saccade was observed per response. Similarly, 400% saccades means four saccades were observed on average per response. Additionally, a linear regression analysis between the onset time of the initial saccade and the latency of the vergence response was conducted. Correlation was quantified with the Pearson correlation coefficient or *r* value using MATLAB™. Figures were generated using MATLAB™ or Excel software.

3. Results

3.1. Vergence peak velocity and initial vergence angle

Typical average vergence step position (unit °) and velocity (unit °/s) traces from four initial vergence angles are shown from subject S2 in Fig. 3. The retinal disparity of the stimulus is the same, yet the dynamics quantified using the peak velocity of the responses vary depending on the initial vergence angle (near or far) and the direction of vergence (convergence or divergence). Average convergence and divergence peak velocities and one standard deviation with an initial vergence angle of near and far for all

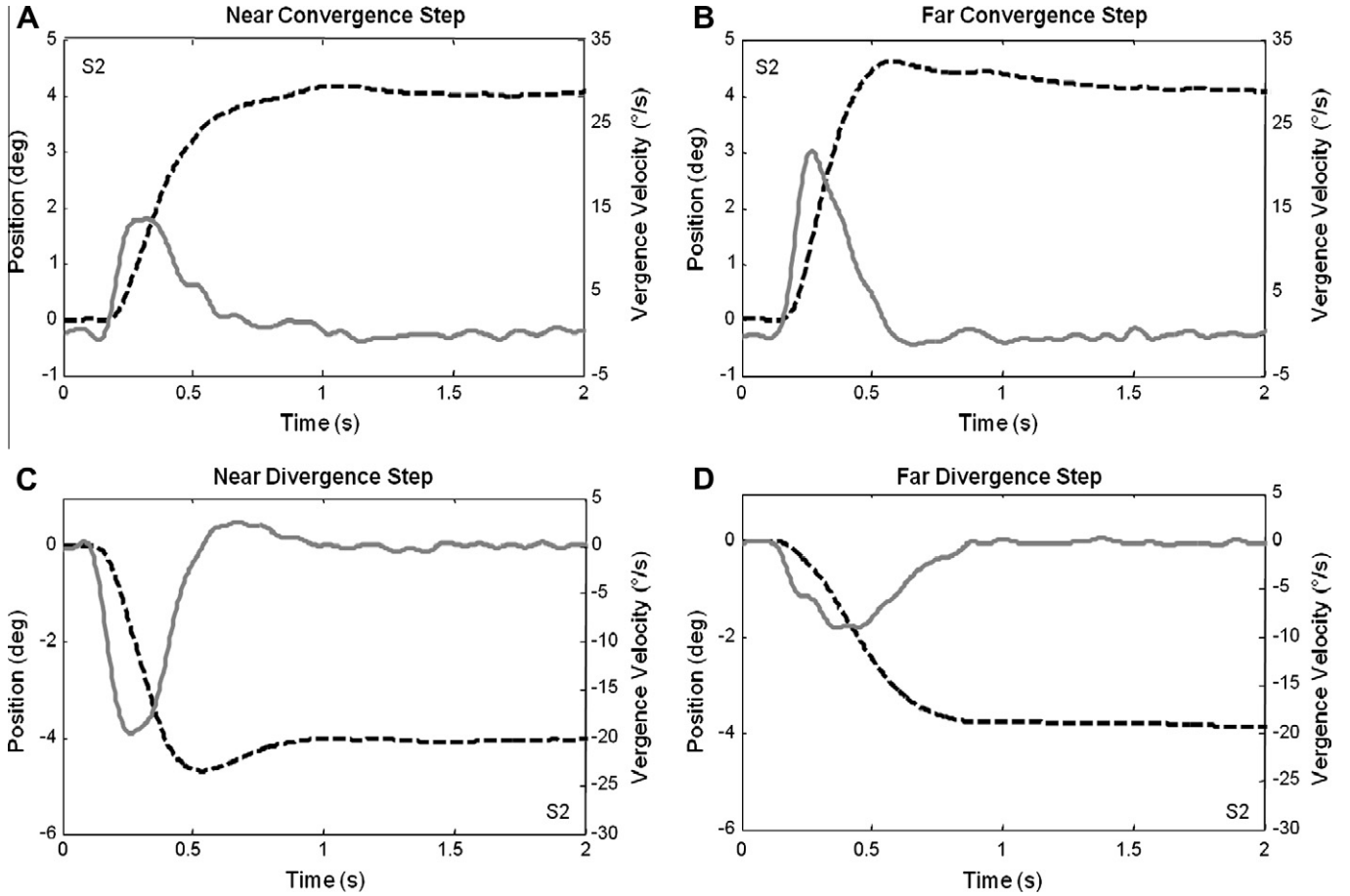

Fig. 3. Average responses from subject S2. Average convergence (black, dashed line) and velocity trace (gray, solid line) from a near initial vergence angle of 12° (plot A) and far initial vergence angle of 2° (plot B). Average divergence (black, dashed line) and velocity trace (gray, solid line) from a near initial vergence angle of 16° (plot C) and far initial vergence angle of 6° (plot D).

ten subjects are plotted in Fig. 4. A repeated measures ANOVA demonstrates that the average convergence (divergence) peak velocity stimulated from the far initial vergence angle were significantly different than the average convergence (divergence) peak velocity stimulated from the near initial vergence angle [$F(1,9) = 7.81$, $p = 0.02$]. The results were confirmed by the post hoc analysis using the Bonferroni all-pairwise test. The data demonstrate that the average convergence peak velocities from a near initial vergence angle (close to the subject) were slower than those from a far vergence angle whereas the average divergence peak velocities from a far initial vergence angle were slower than those from a near vergence angle.

3.2. Correlation between vergence peak velocity and percent of saccades

The group level results of 4° convergence and divergence average peak velocity (°/s) plus one standard deviation stimulated from the near and far initial vergence angles are shown in Fig. 5, plot A for responses without saccade facilitation and those with saccade facilitation during the transient portion (saccades occurring between the vergence latency and the first 400 ms). The average peak velocities of the saccade facilitated vergence responses were greater than the average peak velocity of the responses without saccades during the transient. A trend was observed using a paired *t*-test of the average peak velocity per subject for responses with and without saccade facilitation but significant differences were not observed between the peak vergence velocities ($p = 0.07$). The average percent of saccades in vergence responses plus one standard deviation are shown in Fig. 5, plot B for the three different time periods: (1) from the latency to 400 ms or the transient portion, (2) from 400 ms to 1 s and (3) during the steady state (from 1 to 3 s duration) of vergence responses. Saccades were not observed during the latency of the responses.

The results demonstrate that vergence responses with faster peak velocities (the far convergence and near divergence step responses) have a reduced percentage of saccades compared to vergence responses with slower peak velocities (the near convergence and far divergence step responses). A group regression analysis between the vergence peak velocities and the percent of saccades revealed significant inverse correlations within the transient ($r = -0.41$; $p = 0.008$), from 400 ms to 1 s ($r = -0.35$; $p = 0.03$) and the steady state ($r = -0.44$; $p = 0.005$) portions of the responses. We also performed regression analyses using individual subject data between the vergence peak velocities and the percentage of saccades to reduce the inter-subject variability present within the group data. Regression analyses between vergence peak velocity and percent of saccades in vergence trials for all subjects are shown in Fig. 6. Individual data results demonstrate that the average vergence peak velocities were inversely correlated to the percent of saccades in the transient portion ($r = -0.69 \pm 0.18$), from 400 ms to 1 s ($r = -0.85 \pm 0.12$) and during the steady state between 1 and 3 s ($r = -0.72 \pm 0.19$) of the vergence response in all vergence trials.

3.3. Initial and secondary saccades in symmetrical vergence

For all subjects, we quantified the average onset time of the initial saccades relative to the onset time of vergence stimulus shown

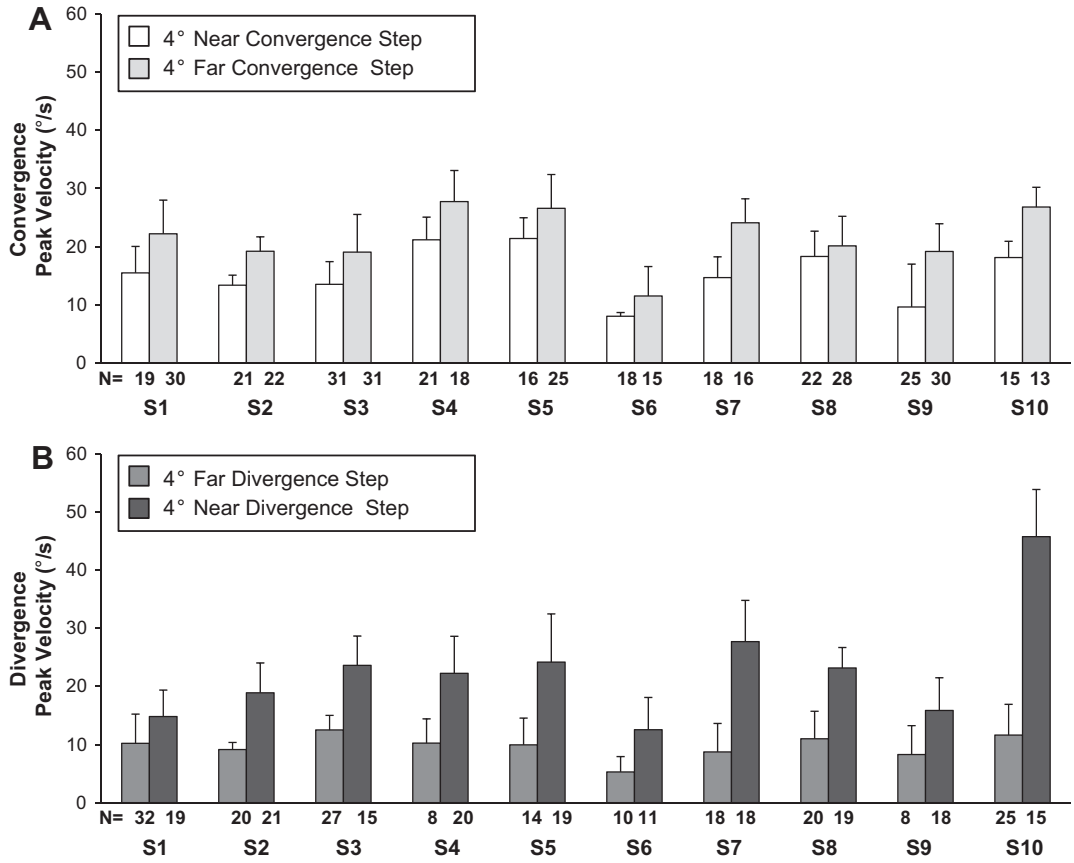

Fig. 4. A summary of average peak velocities (°/s) with one standard deviation of 4° convergence steps per subject (plot A) with an initial vergence angle of 12° (white) and 2° (light gray). Data from 4° divergence steps (plot B) with an initial vergence angle of 6° (medium gray) and 16° (dark gray). The number of samples is reported below the plotted data.

in Fig. 7 plots A and B. We wanted to distinguish whether the onset time of the initial saccades were associated with either the direction of vergence steps (convergence or divergence) and/or the initial vergence angle (near or far). A repeated measures ANOVA demonstrated that a trend was observed between the onset time of initial saccades and the far and near initial vergence angles [$F(1,9) = 4.43$, $p = 0.06$]. However, the onset time of initial saccades were statistically different depending on the direction (convergence or divergence) of the vergence steps [$F(1,9) = 23.93$, $p = 0.0008$]. The average onset time of the initial saccades in convergence responses occurred significantly later compared to the saccadic onset within the divergence responses. These results were confirmed by the post hoc Bonferroni all-pair-wise test. The latency of convergence and divergence for the near and far initial vergence angles are shown in Fig. 7 plots C and D. A linear regression analysis using the Pearson correlation coefficient showed that the timing of the initial saccades were significantly correlated to the latencies of the vergence responses ($r = 0.45$; $p < 0.003$). In addition, a repeated measures ANOVA demonstrated that the latency of the convergence and divergence responses were significantly different depending on the initial vergence angles [$F(1,3) = 44.84$, $p < 0.005$]. Post hoc Fisher's LSD Multiple-Comparison test revealed that convergence (divergence) at near was significantly different than convergence (divergence) at far. Specifically, the longer the vergence latency the latter the initial saccade was observed within the movement.

We quantified the number of error-reducing saccades occurring between 400 ms and 1 s of the vergence response. The average percentage of error-reducing saccades for near and far convergence was 73.4% and 73.1% respectively. For divergence responses, the average percentage of error-reducing saccades was 79.8% and 35.7% for far and near divergence responses respectively.

4. Discussion

4.1. Percent of saccades is correlated to vergence peak velocity

One goal of this study was to quantify the number of saccades in symmetrical vergence responses to determine whether the percentage of saccades in vergence was correlated to vergence peak velocity. The results demonstrate that the prevalence of saccades in all vergence responses was inversely correlated to the vergence peak velocity. Hence, a greater number of saccades were observed in slower vergence movements compared to faster vergence movements in response to symmetrical vergence stimuli.

According to the Dual Mode model, the transient (preprogrammed) component of the vergence system quickly facilitates the movement of the eyes to fuse a binocular target (primarily responsible for the system's peak velocity), while the sustained (feedback) component reduces the error between the current position of the eyes and the target (primarily responsible for system's accuracy) (Horng et al., 1998; Hung, Semmlow, & Ciuffreda, 1986; Semmlow et al., 1993; Semmlow & Yuan, 2002). Our laboratory has used a blind source separation technique to separate the transient from the sustained component and observe that the magnitude of the transient component is significantly correlated to the peak velocity during the transient portion (<400 ms) of the movement (Alvarez et al., 2009; Castillo et al., 2006; Semmlow, Alvarez,

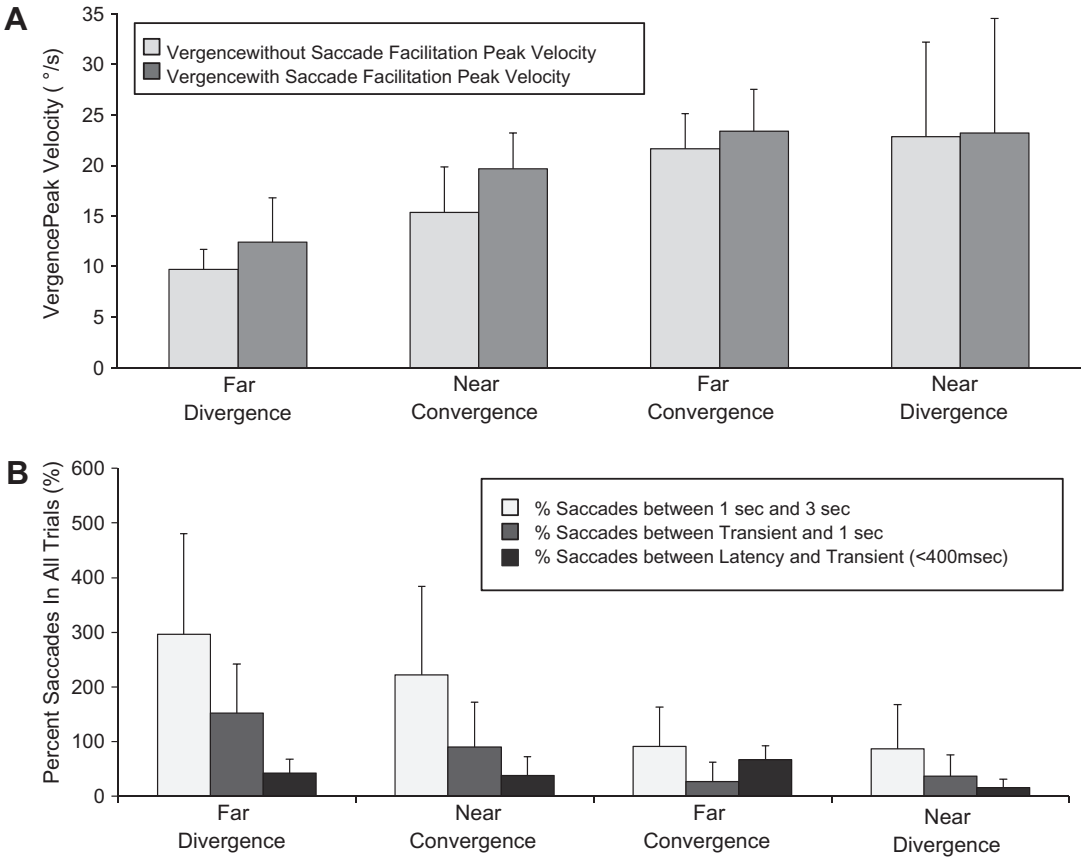

Fig. 5. Group-level results: 4° convergence and divergence average peak velocity (°/s) plus one standard deviation at near and far for all subjects (plot A). Only vergence responses where the peak velocity was not obstructed by a saccade were analyzed. Furthermore, average vergence peak velocities with one standard deviation are plotted for responses with saccade facilitation during the transient (first 400 ms) (medium gray) and those without saccade facilitation during the transient (dark gray). The percent of saccades is defined as the number of saccades present in all vergence trials. The average percent saccades plus one standard deviation during the steady-state between 1 and 3 s of the response (white), between 400 ms and first 1 s (light gray) and the transient portion (from the latency to 400 ms) (dark gray) are shown in plot B.

& Pedrono, 2007; Semmlow & Yuan, 2002; Semmlow, Yuan, & Alvarez, 2002). Hence, we hypothesize that a saccade may have been initiated to facilitate the magnitude of the transient (preprogrammed) portion of the response which may enhance the peak velocity of the vergence movement. In addition, the slower movements have an increased duration of diplopia compared to faster movements which may stimulate the greater prevalence of saccades within slower vergence movements. The current data demonstrate that the prevalence of saccades during the transient portion of all vergence responses and vergence peak velocities were significantly correlated ($r = -0.41$; $p = 0.008$).

Between the 400 ms (after the transient) and the first second, saccades were also observed and were significantly correlated with vergence peak velocity ($r = -0.35$; $p = 0.03$). This significant correlation is probably due to error-reducing saccades in response to the error-inducing saccades observed within the transient portion of the response. A high prevalence of secondary saccades following the initial error-inducing saccades was observed where approximately three quarters of the initial error-inducing saccades were followed by secondary saccades which reduced the error. These results confirm observations of secondary error-reducing saccades within vergence responses stimulated from symmetrical stimuli from other studies (Semmlow et al., 2008, 2009).

Interestingly, the prevalence of saccades that occurred within the steady state (approximately 1–3 s) were significantly correlated to vergence peak velocities ($r = -0.44$; $p = 0.005$). Our laboratory has shown that the sustained component is active within the later segment of the transient portion of the movement (Alvarez et al., 1999). However, it is not fully understood how the preprogrammed and feedback component interact. In addition, when a response has a reduced peak velocity, it is unknown whether the gain of the feedback component is influenced. The rationale for the series of saccades observed within the steady state is not well understood.

4.2. Characteristics of initial saccades induced from symmetrical vergence stimuli

We quantified the onset time relative to the vergence response of the initial saccades. Semmlow et al. (2008) reported that initial saccades occurred 0.2–0.3 s after the convergence stimulus located at an initial vergence angle of 4° while Ying and Zee (2006) reported that initial saccades occurred 0.17–0.77 s after the onset of divergence responses with an initial vergence angle of 30° (Semmlow et al., 2008; Ying & Zee, 2006). However, neither study measured both convergence and divergence responses so this difference in latency range may be due to physiological variation between subjects. Our study shows the average onset time of the initial saccades occurred earlier for divergence compared to convergence responses at the far vergence initial angle. A similar trend (eight out of ten subjects) was observed for the near initial vergence angle. Previous studies have shown that convergence has longer latencies compared to divergence (Alvarez, Semmlow, & Pedrono, 2005; Yang, Bucci, & Kapoula, 2002). Our correlation analysis showed that the differences between the onset time of saccades in convergence and divergence responses were significantly correlated to the latency of the convergence and divergence

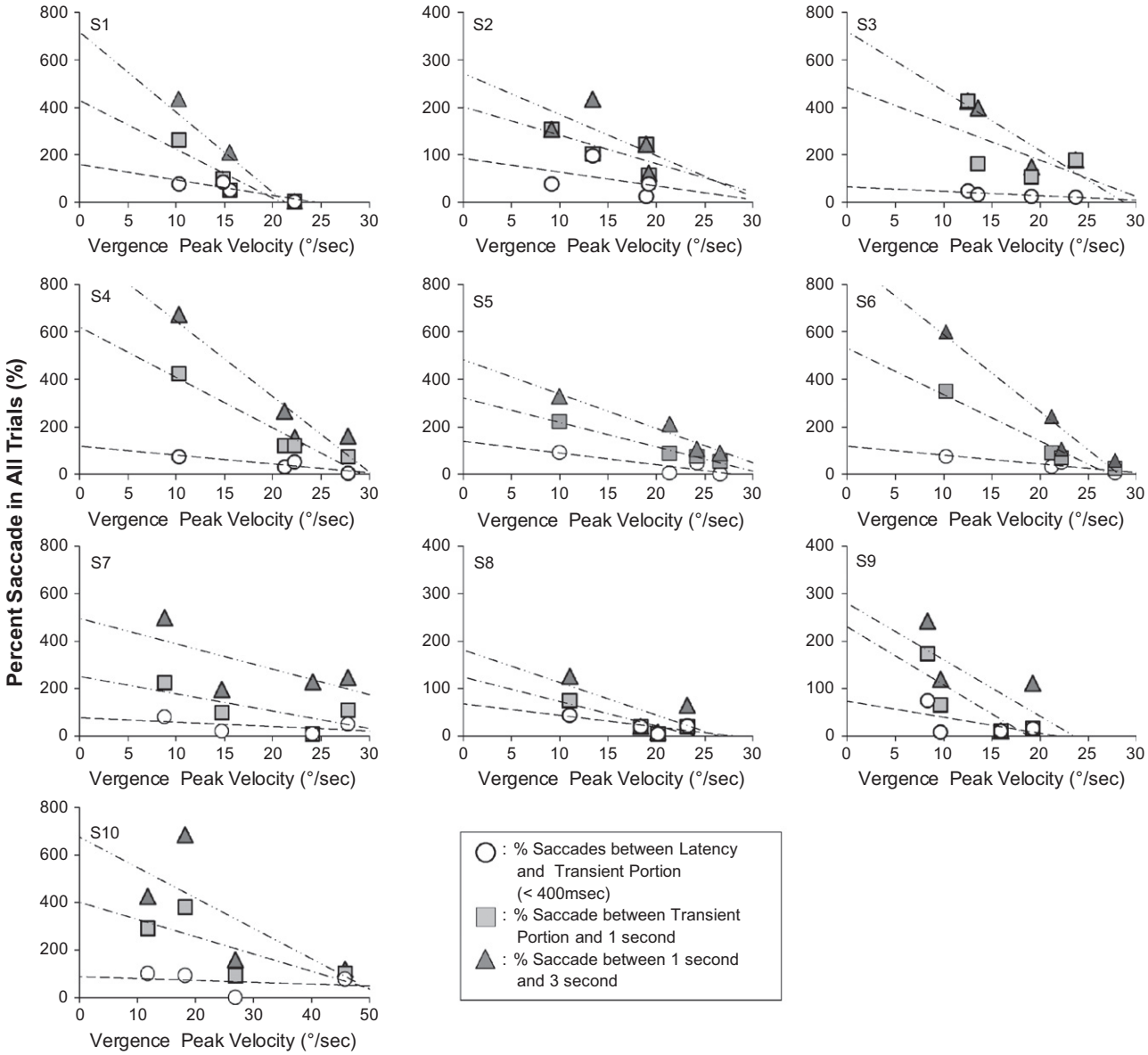

Fig. 6. Linear regression plots of the percentage of saccades in all trials between the latency and the transient portion (less than 400 ms) (white, circle), between the transient portion and the first 1 s (light gray, square), and between the first 1 s and 3 s of the response (gray, triangle) as a function of average vergence peak velocity (°/s) for all ten subjects.

movements ($r = 0.45$; $p < 0.003$). Specifically, the initial saccade was observed latter for vergence movements with longer latencies.

4.3. Vergence peak velocity is dependent on initial vergence angle

In the current study, we randomly presented convergence and divergence steps at far and near initial vergence angles to all subjects. The results demonstrate that both convergence and divergence steps are dependent on initial vergence angle. Patel's model predicts that with equal parameters for vergence, divergence with a near initial vergence angle would be faster than divergence responses stimulated from a far initial vergence angle (Patel et al., 1997). On the contrary, convergence responses stimulated from a far initial vergence angle would be faster than convergence responses initiated from a near initial vergence angle. In a subsequent behavioral study by Patel and colleagues, they report that divergence was dependent on initial vergence angle but this dependence was not observed for convergence (Patel et al., 1999). Alvarez et al. (2005) also reported a similar finding where divergence peak velocities were significantly dependent on the initial vergence angle whereas convergence peak velocities were not dependent on the initial vergence angle. We recently published that sustained fixation of 3–5 min, which evokes phoria adaptation, influences the peak velocity of divergence and convergence and report that convergence and divergence are dependent on initial vergence angle (Kim et al., 2011; Lee et al., 2009). We speculate that one possible reason for observing a strong dependence between the convergence peak velocity and the initial vergence angle, which was not observed in all of the previous reports, is due to a greater initial vergence angle range. Our current study used a range between 2° and 16° which is larger than previous studies (Alvarez & Gayed, 2006; Alvarez, Semmlow, & Pedrono, 2005; Patel et al., 1999). The results presented in the current study support that both divergence and convergence responses are dependent on initial vergence angles.

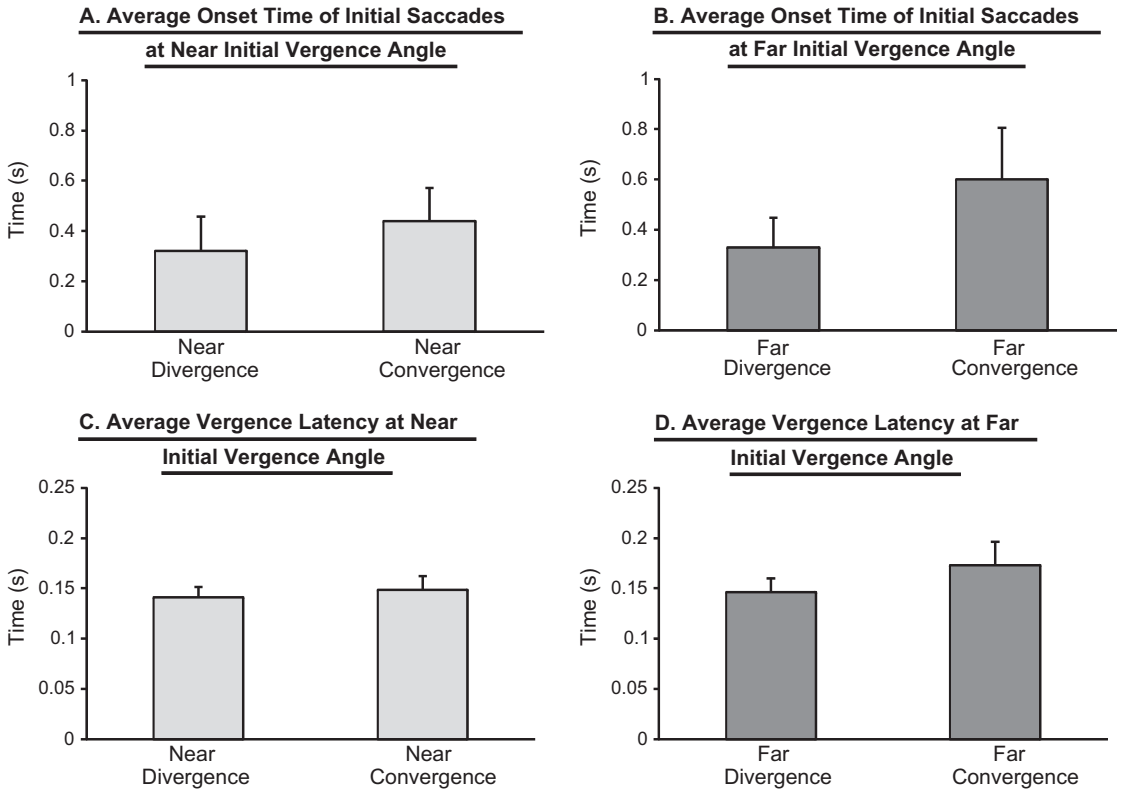

Fig. 7. Average onset time (s) with one standard deviation of the initial saccade observed during responses to symmetrical divergence and convergence stimuli located at the near initial vergence angle (plot A) and the far initial vergence angle (plot B). The average divergence and convergence latency (s) with one standard deviation located at the near initial vergence angle (plot C) and far initial vergence angle (plot D). Latency is defined as the time when the movement begins to show a change in vergence angular position compared to initial vergence angle. The responses analyzed from the near initial vergence angle are shown in light gray and those with the far initial vergence angle are plotted in dark gray.

4.4. Saccade–vergence interaction

Controversies exist in the literature concerning the interaction between saccade and vergence eye movements (Cullen & Van Horn, 2011; King, 2011; Leigh & Zee, 2006). Previous studies have supported that complex, nonlinear interactions exist between the saccade and vergence subsystems (van Leeuwen, Collewijn, & Erkelens, 1998; Zee, Fitzgibbon, & Optican, 1992). Several models have been proposed to describe the enhancement of vergence peak velocity response induced by saccade–vergence stimuli (i.e. looking between targets (side-to-side) that are located in different depths (near to far)). These models are based upon (1) the inhibition of the saccadic omnipause neurons (OPN) (Mays & Gamlin, 1995; Zee, Fitzgibbon, & Optican, 1992), (2) both the saccadic pulse and omnipause neuron inhibition (Kumar et al., 2005, 2006) and lastly, (3) a multiplicative interaction between a weighted saccadic burst signal and vergence motor error (Busettini & Mays, 2005b). However, a recent study by Van Horn and Cullen suggests that the saccadic system, specifically the saccadic burst neurons (SBNs), by itself can encode the saccade facilitated vergence eye movements (Van Horn & Cullen, 2008).

It is important to note that the visual stimuli within our study were pure, symmetrical disparity step stimuli located at different initial vergence angles (i.e. looking at targets located along the subject's midline) and hence had no retinal stimulation to the saccadic system. Yet, saccades were observed, especially within the slower vergence responses. As a result, our data support an interaction exists between the vergence and saccade subsystems. We speculate, based upon the neurophysiology studies, that the responses to symmetrical vergence stimuli (along midline) will evoke the near response cells (Zhang, Gamlin, & Mays, 1991; Zhang, Mays, & Gamlin, 1992) and when the vergence velocity is below a preferred threshold, a saccade may be initiated by (1) the excitation of SBNs, (2) the inhibition of OPNs or (3) both the excitation and inhibition of SBNs and OPNs, respectively. However, future neurophysiology studies are needed to test this hypothesis, to further understand the interaction between saccade and vergence eye movements.

4.5. The neural control of binocular coordination: uniocular or binocular control

Different theories exist in the literature regarding the neural control of binocular movements (Cullen & Van Horn, 2011; King, 2011; Leigh & Zee, 2006; Zhou & King, 1998). One view by Hering suggests that both eyes are equally innervated by common command signals that yoke the eye movements (Hering, 1977). Conversely, Helmholtz argues that binocular coordination is a learned behavior and the left and right eyes are independently controlled (von Helmholtz, 1962).

Although many studies support Hering's law, recent research has reported evidence in favor of Helmholtz's theory (Cullen & Van Horn, 2011; King, 2011). Zhou and King showed that premotor neurons in the paramedian pontine reticular formation, that were thought to encode for saccadic velocity commands, encoded monocular saccadic commands for the left and right eyes (Zhou & King, 1998). In addition, Van Horn and Cullen reported that SBNs carry monocular vergence-related information during disconjugate saccades, further suggesting evidence of uniocular control (Van Horn & Cullen, 2008). However, neither the literature (Cullen & Van Horn, 2011) nor the data presented in this study prove whether

the vergence commands that are required to drive movements in response to symmetrical disparity vergence stimuli (i.e. when the saccadic burst neurons are silent) utilize uniocular control. Future neurophysiology and behavioral studies are needed to investigate whether these two types of responses (saccade-facilitated vergence or pure symmetrical vergence movements in response to symmetrical disparity stimuli) are uniocularly or binocularly controlled. Our results suggest that future neurophysiology studies may consider varying the initial vergence angle to study symmetrical vergence peak velocity with, and without, the presence of error-inducing saccades within the transient portion of the movement to identify which cells modulate their activity with these responses.

5. Conclusion

We assessed whether the frequency of saccades in vergence responses to symmetrical vergence stimuli was correlated to vergence peak velocity. The results show that slower vergence responses have a greater prevalence of horizontal saccades during all temporal segments of the response (transient, 400 ms to 1 s, and steady-state) compared to vergence responses with greater peak velocities. We speculate that the initial saccades are generated to potentially enhance the ongoing vergence movement during the transient portion of the movement. Mostly error-reducing saccades were observed within the 400 ms to 1 s portion of the response, presumably in response to the number of saccades observed within the transient. More neurophysiological research is needed to determine the neural substrate origin generating the greater prevalence of saccades within slower vergence movements. In addition, our results support that convergence and divergence movements are dependent on the stimulus initial vergence angle.

Acknowledgment

Grants: This research was supported in part by NSF CAREER BES-044713 to T.L.A.

References

Alvarez, T. L., Bhavsar, M., Semmlow, J. L., Bergen, M. T., & Pedrono, C. (2005). Short-term predictive changes in the dynamics of disparity vergence eye movements. *Journal of Vision, 5*(7), 640–649.

Alvarez, T. L., Han, S. J., Kania, C., Tsang, O., Kim, E. H., Semmlow, J. L., et al. (2009). Adaptation to progressive lenses by presbyopes. In *NER '09. 4th International IEEE/EMBS conference (Antalya Turkey: 4th international IEEE/EMBS conference)*.

Alvarez, T. L., & Gayed, B. (2006). Divergence dynamic modification as a function of initial position. *Conference of the IEEE Engineering in Medicine and Biology Society, 1*, 5683–5686.

Alvarez, T. L., Semmlow, J. L., & Pedrono, C. (2005). Divergence eye movements are dependent on initial stimulus position. *Vision Research, 45*(14), 1847–1855.

Alvarez, T. L., Semmlow, J. L., Yuan, W., & Munoz, P. (1999). Dynamic details of disparity convergence eye movements. *Annals of Biomedical Engineering, 27*(3), 380–390.

Alvarez, T. L., Semmlow, J. L., Yuan, W., & Munoz, P. (2002). Comparison of disparity vergence system responses to predictable and non-predictable stimulations. *Current Psychology of Cognition, 21*, 243–261.

Alvarez, T. L., Vicci, V. R., Alkan, Y., Kim, E. H., Gohel, S., Barrett, A. M., Chiaravalloti, N., & Biswal, B. B. (2010). Vision therapy in adults with convergence insufficiency: Clinical and functional magnetic resonance imaging measures. *Optometry and Vision Science, 87*(12), E985–E1002.

Bababekova, Y., Rosenfield, M., Hue, J. E., & Huang, R. R. (2011). Font size and viewing distance of handheld smart phones. *Optometry and Vision Science, 88*(7), 795–797.

Bahill, A. T., Kallman, J. S., & Lieberman, J. E. (1982). Frequency limitations of the two-point central difference differentiation algorithm. *Biological Cybernetics, 45*(1), 1–4.

Busettini, C., & Mays, L. E. (2005a). Saccade–vergence interactions in macaques. I. Test of the omnipause multiply model. *Journal of Neurophysiology, 94*(4), 2295–2311.

Busettini, C., & Mays, L. E. (2005b). Saccade–vergence interactions in macaques. II. Vergence enhancement as the product of a local feedback vergence motor error and a weighted saccadic burst. *Journal of Neurophysiology, 94*(4), 2312–2330.

Castillo, C. A., Gayed, B., Pedrono, C., Ciuffreda, K. J., Semmlow, J. L., & Alvarez, T. L. (2006). The transient component of disparity vergence maybe an indication of progressive lens acceptability. *Conference of the IEEE Engineering in Medicine and Biology Society, 1*, 5687–5690.

Collier, J. D., & Rosenfield, M. (2011). Accommodation and convergence during sustained computer work. *Optometry, 82*(7), 434–440.

Coubard, O. A., & Kapoula, Z. (2008). Saccades during symmetrical vergence. *Graefes Archive for Clinical and Experimental Ophthalmology, 246*(4), 521–536.

Cullen, K. E., & Van Horn, M. R. (2011). The neural control of fast vs. slow vergence eye movements. *European Journal of Neuroscience, 33*(11), 2147–2154.

Guo, Y., Kim, E. H., & Alvarez, T. L. (2011). VisualEyes: A modular software system for oculomotor experimentation. *Journal of Visualized Experiments* (49), 2530.

Hering, E. (1977). *Lehre vom binokularen sehen (The theory of binocular vision (1868))*. New York: Plenum Press.

Hoffman, D. M., Girshick, A. R., Akeley, K., & Banks, M. S. (2008). Vergence-accommodation conflicts hinder visual performance and cause visual fatigue. *Journal of Vision, 8*(3), 31–30 (article no. 33).

Horng, J. L., Semmlow, J. L., Hung, G. K., & Ciuffreda, K. J. (1998). Initial component control in disparity vergence: A model-based study. *IEEE Transactions on Biomedical Engineering, 45*(2), 249–257.

Howarth, P. A. (2011). Potential hazards of viewing 3-D stereoscopic television, cinema and computer games: A review. *Ophthalmic and Physiological Optics, 31*(2), 111–122.

Hung, G. K., Semmlow, J. L., & Ciuffreda, K. J. (1986). A dual-mode dynamic model of the vergence eye movement system. *IEEE Transactions on Biomedical Engineering, 33*(11), 1021–1028.

Ishikawa, S. (1990). Examination of the near triad in VDU operators. *Ergonomics, 33*(6), 787–798.

Kim, E. H., Granger-Donetti, B., Vicci, V. R., & Alvarez, T. L. (2010). The relationship between phoria and the ratio of convergence peak velocity to divergence peak velocity. *Investigative Ophthalmology and Visual Science, 51*(8), 4017–4027.

Kim, E. H., Vicci, V. R., Han, S. J., & Alvarez, T. L. (2011). Sustained fixation induced changes in phoria and convergence peak velocity. *PLoS ONE, 6*(6), e20883.

King, W. M. (2011). Binocular coordination of eye movements – Hering's Law of equal innervation or uniocular control? *European Journal of Neuroscience, 33*(11), 2139–2146.

Kumar, A. N., Han, Y., Dell'Osso, L. F., Durand, D. M., & Leigh, R. J. (2005). Directional asymmetry during combined saccade–vergence movements. *Journal of Neurophysiology, 93*(5), 2797–2808.

Kumar, A. N., Han, Y. H., Kirsch, R. F., Dell'Osso, L. F., King, W. M., & Leigh, R. J. (2006). Tests of models for saccade–vergence interaction using novel stimulus conditions. *Biological Cybernetics, 95*(2), 143–157.

Lee, Y. Y., Granger-Donetti, B., Chang, C., & Alvarez, T. L. (2009). Sustained convergence induced changes in phoria and divergence dynamics. *Vision Research, 49*(24), 2960–2972.

Leigh, R. J., & Zee, D. S. (2006). The neurology of eye movements. In *Contemporary neurology series* (pp. 763). New York: Oxford University Press.

Malinov, I. V., Epelboim, J., Herst, A. N., & Steinman, R. M. (2000). Characteristics of saccades and vergence in two kinds of sequential looking tasks. *Vision Research, 40*(16), 2083–2090.

Mays, L. E., & Gamlin, P. D. R. (1995). A neural mechanism subserving saccade–vergence interactions. In J. M. Findlay, R. Walker, & K. R. W. (Eds.), *Eye movement research: Mechanisms, processes and applications* (pp. 215–223). Amsterdam: Elsevier.

Patel, S. S., Jiang, B. C., & Ogmen, H. (2001). Vergence dynamics predict fixation disparity. *Neural Computation, 13*(7), 1495–1525.

Patel, S. S., Jiang, B. C., White, J. M., & Ogmen, H. (1999). Nonlinear alteration of transient vergence dynamics after sustained convergence. *Optometry and Vision Science, 76*(9), 656–663.

Patel, S. S., Ogmen, H., White, J. M., & Jiang, B. C. (1997). Neural network model of short-term horizontal disparity vergence dynamics. *Vision Research, 37*(10), 1383–1399.

Qing, Y., & Kapoula, Z. (2004). Saccade–vergence dynamics and interaction in children and in adults. *Experimental Brain Research, 156*(2), 212–223.

Rosenfield, M. (2011). Computer vision syndrome: A review of ocular causes and potential treatments. *Ophthalmic and Physiological Optics, 31*(5), 502–515.

Semmlow, J. L., Alvarez, T. L., & Pedrono, C. (2007). Dry dissection of disparity divergence eye movements using independent component analysis. *Computers in Biology and Medicine, 37*(7), 910–918.

Semmlow, J. L., Chen, Y. F., Pedrono, C., Alvarez, T. L. (2008). Saccadic behavior during the response to pure disparity vergence stimuli I: General properties. Journal of Eye Movement Research, 1(2), 1–11.

Semmlow, J. L., Chen, Y. F., Granger-Donnetti, B., Alvarez, T. L. (2009). Correction of saccade-induced midline errors in responses to pure disparity vergence stimuli. Journal of Eye Movement Research, 2(5), 1–13.

Semmlow, J. L., Hung, G. K., Horng, J. L., & Ciuffreda, K. (1993). Initial control component in disparity vergence eye movements. *Ophthalmic and Physiological Optics, 13*(1), 48–55.

Semmlow, J. L., & Yuan, W. (2002). Components of disparity vergence eye movements: Application of independent component analysis. *IEEE Transactions on Biomedical Engineering, 49*(8), 805–811.

Semmlow, J. L., Yuan, W., & Alvarez, T. L. (2002). Short-term adaptive control processes in vergence eye movement. *Current Psychology of Cognition, 21*, 343–375.

Thiagarajan, P., Ciuffreda, K. J., & Ludlam, D. P. (2011). Vergence dysfunction in mild traumatic brain injury (mTBI): A review. *Ophthalmic and Physiological Optics, 31*(5), 456–468.

Van Horn, M. R., & Cullen, K. E. (2008). Dynamic coding of vertical facilitated vergence by premotor saccadic burst neurons. *Journal of Neurophysiology, 100*(4), 1967–1982.

van Leeuwen, A. F., Collewijn, H., & Erkelens, C. J. (1998). Dynamics of horizontal vergence movements: Interaction with horizontal and vertical saccades and relation with monocular preferences. *Vision Research, 38*(24), 3943–3954.

von Helmholtz, H. (1962). *Helmholtz's treatise on physiological optics*. New York: Dover Publications, Inc.

Yang, Q., Bucci, M. P., & Kapoula, Z. (2002). The latency of saccades, vergence, and combined eye movements in children and in adults. *Investigative Ophthalmology and Visual Science, 43*(9), 2939–2949.

Ying, S. H., & Zee, D. S. (2006). Phoria adaptation after sustained symmetrical convergence: Influence of saccades. *Experimental Brain Research, 171*(3), 297–305.

Yuan, W., & Semmlow, J. L. (2000). The influence of repetitive eye movements on vergence performance. *Vision Research, 40*(22), 3089–3098.

Zee, D. S., Fitzgibbon, E. J., & Optican, L. M. (1992). Saccade–vergence interactions in humans. *Journal of Neurophysiology, 68*(5), 1624–1641.

Zhang, Y., Gamlin, P. D., & Mays, L. E. (1991). Antidromic identification of midbrain near response cells projecting to the oculomotor nucleus. *Experimental Brain Research, 84*(3), 525–528.

Zhang, Y., Mays, L. E., & Gamlin, P. D. (1992). Characteristics of near response cells projecting to the oculomotor nucleus. *Journal of Neurophysiology, 67*(4), 944–960.

Zhou, W., & King, W. M. (1998). Premotor commands encode monocular eye movements. *Nature, 393*(6686), 692–695.